FIELD MUSEUM OF NATURAL HISTORY
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GEOLOGY, MEMOIRS VOLUME I, NO. 1

STUDIES OF FOSSIL MAMMALS OF SOUTH AMERICA

A PARTIAL SKELETON OF HOMALODONTOTHERIUM FROM THE SANTA CRUZ BEDS OF PATAGONIA

BY

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Blair Professor of Geology and Paleontology
Princeton University

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ELMER S. RIGGS, *in charge*

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BY

WILLIAM BERRYMAN SCOTT

Collected by the Marshall Field Paleontological Expeditions to Argentina and Bolivia, 1922-1927

In the course of the Field Museum expeditions to Patagonia, Mr. E. S. Riggs found in the Santa Cruz formation numerous parts of a skeleton of *Homalodontotherium,* presumably of the species *H. segoviae* Amegh. Owing to the courtesy of Mr. Riggs and Director Simms, of Field Museum of Natural History, this most interesting and important specimen has been confided to me for description. My colleague, Professor W. J. Sinclair, has rendered indispensable assistance in assembling and mounting the scattered parts of the skeleton, thus greatly lightening my labours. Mr. Loris Russell, a graduate student in the Department of Geology, Princeton University, has made the drawings which illustrate this paper. To all of those gentlemen my sincere thanks are due.

The skeleton in question, which was that of a young adult, as is indicated by the epiphyses of the long bones, consists of the skull, with mandible, but lacking the upper surface, one cervical and ten thoracic vertebrae, what is supposed to be a clavicle, parts of the scapula and humerus, the ulna, radius, and carpus complete, three metacarpals and several phalanges of the manus. Of the hinder extremity there are an almost perfect *os innominatum* of the right side, femur, tibia, and fibula. Both hind feet are well preserved, except for the phalanges. Aside from these, the right pes lacks only the calcaneum and the left pes retains the calcaneum, astragalus, navicular, ectocuneiform, and all the metatarsals, but is without cuboid, ento- and mesocuneiforms. By combining the two feet, it is possible to reconstruct the tarsus and metatarsus entirely.

Our knowledge of the Patagonian Entelonychia is so scanty that this additional material is exceedingly welcome and throws much light upon questions which have hitherto been obscure. Though still incomplete, the parts of the skeleton now known suffice to permit a tentative restoration, almost the only uncertainties of which concern the vertebral column; the length of neck, trunk, and tail can be given only conjecturally, though the conjecture is not altogether guesswork. This restoration, so far as it goes, confirms the belief that *Homalodontotherium* was one of the strangest and most bizarre of the Santa Cruz mammals. Its resemblances to the Ancylopoda of the northern hemisphere prove to be less numerous and striking than had been supposed, and were, in my opinion, due to convergent development, not to genetic relationship. In

his later writings, Ameghino assigned the Entelonychia to the Ancylopoda; but this was an ill-advised step, for, as will subsequently be shown, the toxodont characteristics are much more significant.

Though it involves some repetition, this individual, which has been given the Field Museum number, P 13092, will be described in full, without omitting such parts as have been published by Lydekker, Ameghino, and myself, save only the skull and dentition. These have been so completely made known, that no purpose would be served by repeating the descriptions here. The skull, however, of this individual, serves to correct certain misconceptions due to the crushing downward of Ameghino's otherwise fine specimens.

The skull before us has suffered the loss of all the upper part, but the missing region may be readily and confidently restored from other skulls. So completed, and with the mandible in place, this skull immediately reminds the observer of *Diadiaphorus*, the largest of the known Santa Cruz Litopterna. The specimen in the Ameghino collection which he figured[1] and which is also shown on Plate XX of my account of the Entelonychia, though very complete, except that it lacks the mandible, is distorted by vertical crushing, giving quite a false impression of its appearance in side view. This skull has such short nasals as to suggest the existence of a proboscis, an inference which is supported by the great length of the fore limbs. If the creature really had a proboscis, there would be a remarkable prevalence of this organ among the Santa Cruz mammals, not less than three different groups possessing it: *Theosodon* among the Litopterna, the Astrapotheria, and the Entelonychia.

Vertebral Column. The axis has been figured and briefly described by Lydekker.[2] He says: "Although the arch is nearly entire, the centrum has lost its hinder extremity, but the transverse process, perforated by the lateral canal, still remains, and the whole length of the centrum can be approximately estimated. The centrum was proportionately longer than in *Toxodon*, its length being about 4.6 and its anterior width 4 inches. As in all the less specialized ungulates, the odontoid process is peg-like in form." To this may be added that this axis differs from that of *Nesodon* in its relatively greater length and, more especially, in the much greater development of the neural spine, which is a great, hatchet-like plate, resembling that of the Carnivora in form.

The only other cervical that is available for description is apparently the seventh of the series (Plate I, Fig. 3). The neural arch and zygapophyses are nearly complete, but the spine is broken away at its base, and of the centrum only the floor of the neural canal remains. This suffices to show that the centrum was relatively short; the neural canal is large and of D-shaped outline; the zygapophyses are very large and of the usual cervical type. On each side, the anterior and the posterior one are closely approximated, separated merely by a notch. Part of the left transverse process remains, and this seems to have been simple, without inferior lamella. On the posterior surface of the transverse process is a pit, but there is no canal for the vertebral artery.

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[1] F. Ameghino, '94, p. 66, Fig. 23.

[2] R. Lydekker, '93, p. 45, Pl. XX, Fig. 5.

Ten *Thoracic Vertebrae* are associated with the specimen, and these were derived from the anterior, middle, and posterior portions of the thorax. The first thoracic has a short, heavy, and slightly opisthocoelous centrum, which measures 47 mm in length. The neural arch, spine, and prezygapophyses are of the cervical type; and the spine, though broken off at the base, was apparently of no great height. The postzygapophyses are of the thoracic pattern and present directly downward from the ventral side of the neural arch. The facets for the heads of the first pair of ribs are large and deeply concave, those for the second pair much smaller. The transverse processes are very long and massive, and have very large and deeply concave facets for the tubercles of the first pair of ribs. The other anterior thoracic vertebrae are not especially peculiar; they have progressively diminishing centra and transverse processes, on which the facets for the rib-tubercles grow smaller and shallower. The neural canal grows smaller and more cylindrical in shape, becoming exceedingly small in the middle and posterior part of the thoracic region. In none of these anterior vertebrae is the neural spine preserved, but the fractured surfaces indicate that these spines were remarkably short and weak in comparison with the size of the animal. This inference is confirmed by a well-preserved vertebra, with nearly complete spine, which must approximately be the 12th or 13th of the series. The shortness and slenderness of these spines is in notable contrast to the very long and heavy spines of *Nesodon*, which had a prominent hump at the shoulders.

In the posterior thoracic region, the centra again grow progressively larger, though the neural canal remains singularly small. The transverse process grows more and more slender, losing the rib-facets, until on the last thoracic it is short and rod-like. (Plate I, Fig. 5.) The metapophyses first appear on the 12th or 13th vertebra and enlarge rapidly, until, in the last, they are exceedingly prominent, larger and heavier than the transverse processes. The postzygapophyses of the last thoracic are of the lumbar pattern, but are only slightly convex: lacking all the lumbars, it is impossible to say whether they took on the semicylindrical, interlocking form which is characteristic of the Artiodactyla and appears also in *Nesodon* and other toxodonts. This last thoracic has a well-preserved spine, which is quite of the usual lumbar shape, short, broad anteroposteriorly, thin and plate-like transversely. All of the thoracic spines have a backward inclination; if there was any anticlinal vertebra, it must have been in the lumbar region. The length of the centrum of this vertebra is approximately 46 millimeters.

The *Ribs* are represented by three or four complete ones and by many fragments. Those of the first pair are remarkable for the way in which they widen distally, making broad, plate-like bones, with convex lateral, or anterior, and concave medial surfaces. Succeeding ribs grow rounder and stouter, and the posterior pairs become relatively slender. Except for a few of the anterior ones, the ribs do not have the broad, slab-like shape usual in large hoofed-animals.

The *Sternum* is very peculiar. The presternum, or manubrium (Plate II, Fig. 6), is different from any with which I have been able to compare it; its anterior, or free border is much broken, but appears to have been straight, and

the whole anterior part of the bone is broad, depressed, and dorso-ventrally thin, slightly concave on the dorsal side, decidedly convex and keeled on the ventral. Posteriorly the bone narrows and thickens much, so that the hinder surface, for articulation with the first mesosternal segment, has a nearly circular outline. There are two large and deeply concave pits to receive the costal cartilages of the first pair of ribs.

The presternum of *Nesodon* is of an altogether different type,[1] being compressed and narrow transversely, thick dorso-ventrally, and ending in front in a rounded edge. In the Perissodactyla, including the suborder Ancylopoda, the manubrium is characteristically thin and deep; but neither these animals, nor the Artiodactyla, have a presternum at all like that of the Entelonychia.

The *mesosternum* of the present skeleton is made up of an indeterminate number of segments, only three of which are preserved. The foremost mesosternal segment cannot be one of those present, for the hinder end of the manubrium demands, for articulation, a shape quite unlike any that remains. Such of the segments as have been collected are remarkably broad, flat, and thin dorso-ventrally. The last segment, or xiphisternum, is very broad anteriorly, where it articulates with the last mesosternal segment, and contracts rapidly to a narrow posterior portion.

The *Clavicle* is listed as one of the parts of this specimen. There is nothing *a priori* improbable in the retention of a clavicle in the present group, as it is retained in the allied suborder of the Typotheria. The Entelonychia have many primitive features, such as the pentadactyl manus, and, as will be subsequently shown, Lydekker was very probably right in his suggestion that *Homalodontotherium* was fossorial in its habits. Such a way of using the fore foot almost necessitates a clavicle; and, finally, the elbow joint and the shape of the radial head make it exceedingly probable that there must have been some power of pronation and supination. On the other hand, no place has been found on the sternum or the scapula for articulation with a clavicle. In view of the state of preservation of these bones, this is not a conclusive objection. The bone is short, irregularly cylindrical, and twisted for most of its length, and the two ends are very different from each other; one is broad, thin, and plate-like, the other cylindrical, with roughened end-surface. No evidence of articulation is distinctly visible on either end. (Plate II, Figs. 9, 9a.)

Appendicular Skeleton. The *Scapula* is represented by a large fragment, too incomplete to allow the shape of the blade to be determined. (Plate III, Figs. 10, 10a.) The glenoid cavity is present on another fragment, but the coracoid and acromion have been lost. The large piece, which has the spine for nearly its entire length, is, except for its much smaller size, very like the imperfect scapula of *Astrapotherium* which I have described and figured,[2] though the latter has a nearly intact acromion. As in the latter genus, the spine is very prominent, becoming higher and higher distally; the external or free border of the spine is, as in *Astrapotherium,* broad and roughened by obscure longitudinal

[1] W. B. Scott, '12, Pl. XXII, Fig. 1.
[2] Scott, '28, p. 323, Pl. XXXVI, Fig. 2.

ridges, but these are less regular and uniform than in the latter. Another resemblance lies in the absence of any metacromion, at least so far as the spine is preserved. In this regard *Astrapotherium* and *Homalodontotherium* agree, and differ from all other known Santa Cruz ungulates. In the suborder Toxodonta, and in the family Macrauchenidae of the Litopterna, there are two long and conspicuous metacromia, though these processes are of quite different shapes in the two groups. In the suborder Typotheria and the family Proterotheriidae of the Litopterna the scapula has a single well-defined metacromion, while in the Astrapotheria and apparently also in the Entelonychia the scapula has no such process.

The limbs and feet of *Homalodontotherium* are extremely peculiar and display several features which are difficult to interpret in terms of function and movement. No other Santa Cruz mammal even remotely resembles this genus in these respects. A certain likeness to the extremities of the equally strange and bizarre Ancylopoda of the northern hemisphere may be noted, but it does not extend beyond a general similarity of the feet; the limb-bones are entirely different. The Ancylopoda are so characteristically perissodactyl in essentials of structure, that they can, at most, be placed as a suborder of that group, while the Entelonychia are a remarkable specialization of a primitive toxodont stock.

On the whole, the fore limb and foot are considerably longer than the hind, so that the back must have sloped more or less steeply from the shoulders to the rump, much as in *Moropus*, of the North American Miocene. The various segments of the extremities are of very different lengths and in proportions not usual among hoofed-animals. The humerus and femur are quite elongate, the fore arm bones extremely long, and those of the lower leg extremely short, while the fore foot is long and the hind foot very short.

The *Humerus* (Plate III, Fig. 11, Plate IV, Fig. 11a), which appears to be shorter than the femur, has moderate elongation in proportion to the size of the animal, and is of a character which is very exceptional among hoofed animals. The Field Museum skeleton has only an incomplete distal end of the humerus, but Lydekker figures a specimen which is complete as to length, though badly damaged in the anterior part of the proximal end. The figure shows a relatively small head and a very large external tuberosity, though it is difficult to make a positive statement concerning it. The shaft is uncommonly massive, both in transverse and in antero-posterior diameters, the latter in part due to the extraordinary development of the deltoid crest. This extends down for three-quarters of the length of the shaft and ends abruptly in a blunt hook, which is slightly curved toward the inner side. The distal end of the crest is very prominent, and projects 3 inches or more in front of the shaft.

Lydekker has emphasized the very unusual character of the deltoid crest, as occurring in an ungulate; he compares its development to that of the Wombat (*Phascolomys*) and believes that it suggests "fossorial powers,"[1] a suggestion which is strongly supported by other features of the anatomy. The distal end is extremely wide, an individual in the La Plata Museum measuring 7.5 inches

[1] Lydekker, '93, p. 46.

in breadth; the Chicago specimen is somewhat narrower, pertaining to a smaller animal. Much of this great breadth is due to the remarkable extension of the supinator ridge, and the large, prominent, and rugose entepicondyle, which is imperforate. The trochlea is low and very simple in form, and quite saddle-shaped, concave transversely and convex antero-posteriorly. The anconeal fossa is wide and low and very deep, but does not perforate the bone.

Lydekker has compared this humerus to that of *Phascolomys;* to me it suggests a gigantic Mole, though so large an animal could hardly have been a burrower; the question of habits will be discussed in connection with the restoration (p. 26, Plate VII). The measurements of the two specimens mentioned above are as follows:

Humerus, estimated length (L.P.M.)	M.0.400
Humerus, estimated length (F.M.N.H.)	.372
Humerus, estimated distal width (L.P.M.)	.175
Humerus, estimated distal width (F.M.N.H.)	.165

The humerus of *Astrapotherium* has no resemblance to that of *Homalodontotherium* and is much more like that of an enlarged *Nesodon.* It is relatively much more slender and elongate, and has no such development of the deltoid crest and supinator ridge. While the humerus of the Santa Cruz Entelonychia strongly suggests fossorial habits, that of *Astrapotherium* indicates the normal ungulate method of locomotion. The same is true of *Moropus,* the humerus of which is so typically perissodactyl, as to hint at no relationship with the Entelonychia.

The bones of the fore arm are very long and slender in comparison with the other limb-bones, humerus, femur, and tibia.

The *Radius* (Plate IV, Fig. 15) is a curious, irregularly shaped bone; the proximal end is not at all like that of other ungulates, in which the elbow joint is ginglymoid, but is narrow and discoidal, so as to indicate some power of rotation. The proximal facet for the ulna is transversely convex and covers most of the posterior part of the radial head. On the antero-external side of the head is a large convex surface, evidently articular, which was probably for a radial sesamoid, as it cannot be brought into articulation with the ulna or the humerus. The shaft is irregularly curved forward and inward, with slightly convex anterior surface and concave posterior one. Both lateral borders are sinuous in outline and on the external side is a rugose, interosseous crest, an inch or so in length and some 3 inches below the proximal end.

The distal end (Plate IV, Fig. 15b) is quite massive, exceeding the proximal end, not so much in breadth, as in thickness. The anterior surface is very rough, and there is a broad, obscurely marked tendinal sulcus, and a deep notch indicates the inner border of the lunar facet. The surface for articulation with the carpus is of very unusual type; the facets for the scaphoid and lunar are not separated by any visible line, but form a continuous surface along the dorsal border of the distal end, and this surface is transversely concave, less so palmodorsally. The facet for the lunar has twice the dorso-palmar diameter of that for the scaphoid, and this surface is quite deeply concave. A large and deep sulcus invades the articular surface from the inner side, giving the lunar facet a

strongly concave inner border. This sulcus opens anteriorly into the notch of the dorsal border already mentioned. The distal facet for the ulna is small, transversely oval, and nearly plane. The length of this radius is M.0.418.

The radius of *Astrapotherium* is, as yet, incompletely known, little more than the proximal and distal ends being represented in the Princeton collection. These fragments, however, suffice to show that in this genus the radius is of an altogether different type from that of *Homalodontotherium.* The surface for articulation with the humerus is much more extended transversely, is far more complex in form, and is so interlocked with the humeral trochlea, as to preclude any possibility of rotation, and the proximal part of the shaft is much more slender. The distal end is larger, and its carpal surface is simple, without any invading sulcus.

In *Moropus*, also, the radius is so different from the Entelonychian type and so normally perissodactyl, as to require no description here.

The *Ulna* (Plate IV, Fig. 16) is, of course, very long and decidedly curved, so that the inner side is concave and the outer correspondingly convex for its whole length. The olecranon is greatly elongated and extends upward in the line of the shaft, hardly projecting at all behind it. The sigmoid notch forms rather less than a semicircle, and has a very broad articular surface for the humerus. The only facet for the humeral trochlea is the inner one, as the radius covers the whole external portion of the trochlea. The shaft is less distinctly trihedral than is usual in the ungulates, and tapers very gradually downward. On the inner side of the distal end is a small, slightly convex, surface for the radius and, below this, the ulna contracts to half its diameter and bears an oblique, somewhat convex facet for the cuneiform. This is confined to the distal and radial aspects of the bone, and is not reflected over upon the palmar side; apparently there was no contact with the pisiform.

In total length this ulna measures M.0.517.

The ulna of *Astrapotherium* is, as yet, known only from fragments, but these display a number of important and characteristic differences from that of *Homalodontotherium.* The articular surface of the sigmoid notch is wider, and the internal facet for the humeral trochlea is narrower, but is prolonged anteriorly considerably more, and there is a distinct, though much smaller, external facet, which is not present at all in the other genus. The proximal part of the shaft is relatively thicker antero-posteriorly, and the distal end is entirely different; the facet for the cuneiform is far wider transversely, and the articular surface, presumably for the pisiform, is reflected far up upon the palmar side of the ulna.

Comparing the fore-arm bones of the two genera, we find nothing to suggest that they are at all closely related.

Of the *Manus* (Plate III, Fig. 12), the carpus is completely preserved, with the exception of the trapezium and pisiform, and the three ulnar metacarpals are represented, the third and fourth of the right side, the third and fifth of the left. A few phalanges, including unguals, were also recovered. All the elements of the carpus are peculiar and unlike those of any other known ungulate. The bones of the first row are conspicuously shorter in the proximo-distal dimension than those of the second row.

The *scaphoid* has a very oblique position (not well shown in the figure) when adjusted to the radius and the other carpals. It has an irregularly nodular shape, and the facets for other bones occupy but a relatively small part of it. On the proximal side is a small, convex, and irregularly-shaped facet for the radius, which covers hardly more than half the breadth of the scaphoid and is invaded from the radial side by a deep sulcus; it is reflected well down over the dorsal face. The remainder of the proximal surface is rugose, as are also the palmar and radial sides. On the ulnar side is a relatively large, convex facet for the lunar. On the distal end is a slightly saddle-shaped facet for the trapezoid, but none for the trapezium or magnum.

The *lunar* is much the largest bone of the upper row and, excepting the unciform, the largest in the whole carpus; it is short proximo-distally, wide transversely, less so palmo-dorsally. The whole proximal end is covered by the strongly convex surface for the radius, which is reflected far down upon the dorsal side. The inner part of this radial surface slopes down more steeply, so as to make an angulation with the outer portion, when the bone is viewed from the front. On the radial side is a large, concave surface for the scaphoid, which is confined to the proximal part of the lunar and projects radially conspicuously beyond the distal half of the bone. The articulation with the cuneiform is confined to a narrow distal facet; proximally, there would seem to have been no direct contact between these two carpals, as is also true of *Nesodon*. Distally, the lunar rests upon the magnum and the unciform; the surface for the magnum is much the larger, but very oblique, and almost as much lateral as distal. On the dorsal side, the surfaces for the magnum and unciform form an obtuse angulation. That for the magnum is complex, the smaller dorsal portion being transversely concave, while the much larger palmar portion is deeply concave in both dimensions, but passing into a nearly plane surface at the radio-palmar angle. The surface for the unciform is more distal and slightly convex; it narrows much posteriorly, the palmar portion being hardly half as wide as the dorsal.

The *cuneiform* is considerably larger than the scaphoid, smaller than the lunar. The whole proximal end is occupied by the nearly plane surface for the ulna, and the whole distal end by that for the unciform, which is slightly concave transversely. The facet for the lunar is confined to the distal portion of the radial side, and is bounded proximally by a rather deep sulcus. The facet for the pisiform is very large and covers nearly the whole palmar side of the cuneiform; it is decidedly concave proximo-distally, and the distal portion projects prominently backward.

The *trapezium* is not preserved in the Field Museum specimen, but it is figured by Ameghino, who shows it to be a small bone, resting laterally against the trapezoid.

All the other carpals of the second row, trapezoid, magnum, and unciform, are much elongated proximo-distally, in marked contrast to those of the upper row, thus differing markedly from the carpus of *Nesodon,* in which these proportions are reversed.

The *trapezoid* is a peculiar-looking bone; it is high proximo-distally, broad transversely, and very thin palmo-dorsally, except for a massive projection from

the radio-palmar angle. The entire proximal end is covered by the surface for the scaphoid, which is irregularly concave and oblique, descending toward the radial side and curving in the palmar direction. The radial portion of this surface, about one-third of the whole, is abruptly narrowed. The articulation with the magnum, which is of unusual character, is by means of two widely separated facets. The first of these is a narrow band, running for the whole proximo-distal height of the bone and near the dorsal border. The second facet is a small, plane, D-shaped surface, which is placed on the ulnar side of a distal projection from the palmar side of the trapezoid. The distal facet for metacarpal II is also divided into two parts, a dorsal one which is broad and shallow, and a much narrower palmar one, which has great antero-posterior extension. When the trapezoid and magnum are placed together in their natural positions and viewed from the distal end, it is seen that in each of these carpals, the surface for mc. II is separated into dorsal and palmar portions by a deep sulcus, which forms an irregularly cylindrical passage for the whole proximo-distal diameter of these bones and appears on the proximal side. On the radial side is a large facet for the trapezium, which has an oblique latero-distal position and is confined to the distal part of the radial side. This facet forms two branches, with a deep, circular pit between them.

The *magnum,* though having nearly the same proximo-distal length as the trapezoid, is a much larger and heavier bone, exceeding the latter chiefly in dorso-palmar thickness. Its anterior, or dorsal, face is irregularly quadrate in outline and has a rugose texture. The whole proximal end is covered by the irregularly saddle-shaped surface for the lunar. As there is no contact with the scaphoid, the dorsal part of which descends steeply toward the ulnar side, the palmar portion rises into a low convexity, which obscurely represents the "head" of the magnum, which is much more distinct in most other ungulates. On the radial side are two facets for articulation with the trapezoid, which correspond closely to the two facets, already described, on the ulnar side of that bone. The surface for the unciform is in two branches, which meet nearly at a right angle; one branch is almost vertical and forms a band near the dorsal border; the second branch is horizontal and proximal and, near the palmar side, it laps over on the unciform. The two branches enclose a large pit, with rugged bottom. The whole distal end of the magnum is occupied by the broad, saddle-shaped surface for the head of mc. III. In addition, there are two small, lateral facets for the head of mc. II; these are quite widely separated by the same sulcus which separates the facets for the trapezoid, in the manner above described.

The *unciform* is much the largest and heaviest bone of the carpus, and has the six articular surfaces usually seen in the pentadactyl or tetradactyl ungulate manus; viz., those for the lunar, cuneiform, magnum, and mc. III, IV, and V. The principal diameter of the bone is the proximo-distal, though the transverse dimension is nearly as great. Of the two proximal facets, that for the cuneiform is much the larger, very oblique, and of complex curvature. The mode of articulation with the magnum is quite a complicated one; along the dorsal border of the radial side is a narrow, vertical band, which extends for the whole

proximo-distal height of the unciform; the second portion is an oblique surface near the palmar side of the proximal end, and on this the magnum overlaps. The facet for mc. III is quite large, but entirely lateral, as the unciform does not rest at all upon that metacarpal. The surfaces for mc. IV and V cover the distal end and are but faintly demarcated, and are saddle-shaped, convex transversely and concave palmo-dorsally. The facet for mc. V is extended up on the ulnar side of the unciform almost to a contact with that for the cuneiform, and this lateral portion has hardly more than half the dorso-palmar diameter of the distal portion.

The arrangement of the elements in this carpus is neither completely interlocking, nor yet entirely serial. Adapting Cope's term, it may be called semi-taxeopod, for, while the lunar rests upon both magnum and unciform, the scaphoid is supported only by the trapezoid, touching neither trapezium nor magnum. Similarly, the carpo-metacarpal articulations are of very simple character; except, of course, the unciform, no carpal directly rests upon more than one metacarpal, and contact with any other is entirely lateral. Metacarpal I articulates only with the trapezium; upon mc. II the trapezoid rests, and contact with the magnum is lateral; and mc. III, supporting the magnum, abuts against the unciform.

The *Metacarpus* is not yet completely known, for no entire example of the first metacarpal has been found. Ameghino's specimen retains the proximal end, which shows that the bone must have been very slender, but leaves the question of its length uncertain; it can hardly have been more than a functionless vestige.

Metacarpal II is likewise known only from the proximal end, most of the shaft being wanting, but its shape can be approximately restored. Metacarpals III, IV, and V are completely represented in the Field Museum skeleton; these bones are remarkably slender and elongate, and form a most curious contrast to the short and sturdy metatarsals. All of the metacarpals, except perhaps the first, have a very exceptional type of distal trochlea and articulation with the phalanges of the first row, which I have not seen repeated in any other mammal. The trochlea has a backward, or palmward, curvature and projection, which brings its anterior surface far behind the dorsal side of the shaft. The articular surface for the first phalanx is continued proximally into a concavity on the distal end of the shaft, which is deepest and most conspicuous on mc. III, while the carina is confined to the palmar side and is almost obsolete. This curious trochlea and the corresponding surface on the first phalanx indicate an uncommon degree of mobility in the digits and are altogether unlike the structure displayed in the other groups of ungulates in which the hoofs have been transformed into more or less clawlike shape, viz., the Ancylopoda of the Perissodactyla, and the Agriochoeridae of the Artiodactyla.

Metacarpals III and IV form a nearly symmetrical pair of almost the same length and thickness. When fitted together, however, mc. III rises higher proximally and mc. IV descends lower distally. Metacarpal II and V are not a pair. Each of the four functional metacarpals has, of course, its own characteristics.

Metacarpal III is the longest of the series, slightly exceeding mc. IV in length. On the radial side of the head are two small facets, dorsal and palmar in position, for mc. II, and on the ulnar side, two much larger surfaces, also dorsal and palmar, for mc. IV. The dorsal facet is oblique, for III overlaps the head of IV, to impinge against the unciform by a large plane facet, which is confined to the dorsal part of the ulnar side. The shaft is long and slender, especially when seen from the front, for, except in the middle of its course, the shaft has a more considerable dorso-palmar diameter. The distal end is recurved and projects strongly backward, displacing the whole trochlea toward the palmar side, to make room for the articular concavity on the distal end of the shaft proper, as described above.

Metacarpal IV is almost a replica of III, from which, aside from a few minute details, it differs only in the conformation of the proximal end. The surface for the unciform is rather narrow and somewhat convex transversely, quite deep and slightly concave palmo-dorsally. The only other articulations are with the adjoining metacarpals, for each of which there are two facets, one near the dorsal and the other near the palmar border of the radial and ulnar sides respectively. Those on the radial side, for the head of mc. III, are quite widely separated, but, on the ulnar side, the facets for mc. V are connate, making a continuous articular band, but the connection is very narrow.

Metacarpal V is of nearly the same length as III and IV, but far stouter and heavier than any other metacarpal. The proximal end bears a saddle-shaped surface for the unciform, which extends well up on the ulnar side of the latter, and externally to this surface on the metacarpal arises a massive rugosity. The distal end resembles that seen in the other members of the functional series, but the articular concavity is shallower and the carina even more obsolete.

Measurements of the complete metacarpals are as follows:

Metacarpal III, length	M.0.174
Metacarpal III, prox. width	.0317
Metacarpal IV, length	.169
Metacarpal V, length	.172
Metacarpal V, prox. width	.0388

The *Phalanges* are but scantily represented in the collections, but there is sufficient material to make clear their more important characteristics. (Plate III, Fig. 13.) A phalanx of the first row is short, heavy, very broad proximally, narrowing much distally. The articular surface for the distal end of the metacarpal consists of two parts, a large, shallow, proximal concavity for the trochlea of the metacarpal, which has no groove for the carina, and a convex surface on the dorsal side of the phalanx for articulation with the peculiar concavity on the distal end of the metacarpal shaft above described. This second and very exceptional mode of articulation comes into play only when the digit is folded back to a degree not possible in normal ungulates. On the palmar side of the phalanx, at the proximal end, are two heavy and prominent rugosities for ligamentous attachment. The distal articulation for phalanx 2 is very much narrower than the proximal one, and is divided by a deep median cleft; this

surface is distal and palmar, and is hardly reflected at all upon the dorsal side of the bone.

The second phalanx is much shorter than the first and more uniform in width, though the proximal end is somewhat wider than the distal. The proximal articulation is in two concavities, while the distal one describes more than half a circle and is reflected over upon the dorsal side of the bone for more than half its length. This joint also must have allowed an unusual freedom of motion. This phalanx bears a decided resemblance to the corresponding one of *Moropus*, the principal difference being that in the latter the bone is relatively narrower and much thicker palmo-dorsally.

The ungual phalanx, which again is remarkably like that of *Moropus*, is not exactly a claw, nor yet a hoof; it is too thick and heavy for the former, too narrow and pointed for the other; it is elongate, decurved, strongly convex on the dorsal and slightly concave on the palmar side. The ungual is deeply cleft from the distal end and has a very rugose surface. The articular surface for the second phalanx describes less than half a circle and is very obscurely divided into two concavities. There is no subungual process, but the dorsal surface is prolonged into a heavy, blunt projection which recalls that seen in the Gravigrada. Indeed, when seen from the side, this ungual phalanx has a distinct resemblance to that of one of the Santa Cruz ground-sloths, but, when looked at from above or below, there is little likeness. The ungual of *Moropus* (Plate III, Fig. 14) is relatively shorter and heavier than that of the Santa Cruz genus and, in the latter, the four functional digits would seem to have had phalanges of nearly the same size, though in digit V they were rather larger and more asymmetrical than in the others. So far as can be told from the available material, there was no such enlargement of the claw in any digit as occurs in the second of the fore foot in *Moropus*.

The *Pelvis* (Plate V, Fig. 17), one-half of which is very well preserved, is unlike that of the other known Santa Cruz ungulates, and is especially different from that of *Nesodon*. The ilium is very broad and has a strongly convex anterior border and the gluteal surface is nearly flat. The surface for articulation with the sacrum is surprisingly small and high up on the inner side. Apparently, there was no great strength in this joint, a puzzling circumstance when the size and weight of the animal are considered. The pedicle is short and stout and not very definitely trihedral, though the three borders may be distinguished. The acetabulum is large and deep, but the articular surface is hardly more than a ring, as it is deeply invaded by an unusually large sulcus for the round ligament. The ischium and pubis, in particular, differ in their proportions from those seen in *Nesodon*, being relatively much shorter in the antero-posterior dimension, but having a far greater dorso-ventral extension. The obturator foramen, which in *Nesodon* is an elongate oval, is here of much more nearly equal diameters. The ischium has a short, heavy proximal portion, which expands distally into a very broad and thin plate. The pubis is of similar form and is indistinguishably fused with the ischium, so that the limits of the two elements cannot be definitely de-

termined. The pubic symphysis is not well preserved but would appear to have been quite short.

The dimensions are as below:

Pelvis, length	M.0.467
Pelvis, greatest breadth of ilium	.287

The hind limb is much shorter than the fore limb, but this shortening affects especially the lower leg and foot.

The *Femur* (Plate V, Fig. 18) is not complete on either side, but the two portions together make a combination which is open to very little doubt, the only question being as to the exact length of the shaft. This femur differs so decidedly, and in so many ways, from that in the La Plata Museum, which was described and figured in my account of this genus,[1] that there must have been an error in identification. In the individual before us, the femur is very long (longer than any of the limb-bones except the ulna and radius), broad and flattened antero-posteriorly. Though this flattening is in some degree due to crushing, it agrees with the proportions found in nearly all of the groups of heavy ungulates.

The head is hemispherical and nearly sessile, and has no pit for the round ligament, another resemblance to many massive ungulates of diverse groups. The great trochanter has been broken away and lost, but was evidently low, as is shown by the shallowness of the notch between it and the head. There is no second trochanter, such as is feebly indicated in the La Plata specimen, and the third trochanter is very inconspicuous, forming a low ridge, with thickened and rugose free border, which is greatly elongated proximo-distally. In the La Plata femur the third trochanter is of entirely different character, being very prominent and short proximo-distally. This difference is so decided and so important systematically, that the reference to the present genus is altogether improbable. The digital fossa is deep, and there is a short remnant of the intertrochanteric ridge.

The shaft is long, broad, antero-posteriorly compressed and nearly straight, with only moderately convex external and concave internal border. This is in very marked contrast to the La Plata femur, in which the inner border is so strongly concave. There is no definite supra-patellar fossa. The rotular trochlea is broad, rather shallow, and nearly symmetrical, with borders of almost equal height, and the articular surface is continuous with that of both condyles. The latter are low and differ in form, the internal one being more prominent and more convex than the external. The principal measurement is:

Femur, estimated length	M.0.488

The bones of the lower leg are completely separated, not ankylosed at the proximal end, as they are in *Nesodon;* they are remarkably, grotesquely short, especially when placed beside the very elongate bones of the fore arm.

The *Tibia* (Plate VI, Fig. 21) is very massive, especially the proximal portion, which is of the usual trihedral shape. The condyles are nearly plane and stand at different levels, the external one being higher proximally than the internal. The presence or absence of a spine is a matter of doubt, as that part of the bone is much broken. The cnemial crest is extremely heavy, prominent, and

[1] SCOTT, '28, Pl. XXX, Fig. 3.

massive, and projects far forward, but does not extend very far down the shaft. The distal end is broad and very much compressed antero-posteriorly, giving it a very unusual shape. The surface for the astragalus has a deeply concave internal condyle, which is extended posteriorly into a nearly plane facet for a corresponding one on the astragalus behind, or proximal to, the trochlea. The internal malleolus is short, but very thick and heavy. On the outer side of the distal end is a facet, which overlaps and rests upon the fibula.

The *Fibula* (Plate VI, Fig. 22) is, of course, considerably shorter than the tibia; it is relatively stout and bowed outward, leaving a wide interosseous space. The proximal end is heavy and rough, and bears a large articular surface for the tibia. The shaft is stout, unusually so, indeed, of irregularly trihedral shape and curved, with the convexity outward. The distal end is even more enlarged and massive than the proximal, and forms an uncommonly heavy external malleolus; it has three articular surfaces, which are all connected. On the extreme distal end is a large, plane facet for the calcaneum; obliquely lateral is a concavity for the astragalus, and the third facet, on which the tibia rests, is small and semicircular and inclined obliquely upward. Among ungulates, this ankle joint is of very exceptional character, and is to be correlated with the extremely peculiar structure of the hind foot, which has a certain Edentate likeness. Measurements of the lower leg-bones are as follows:

Tibia, length	M.0.294
Tibia, proximal width	.122
Fibula, length	.272

The lower leg-bones of *Astrapotherium* are as different as possible from those of *Homalodontotherium*, but almost equally peculiar. The tibia is long and remarkably slender and is, in its proportions, curiously like the human shin-bone. The fibula is quite stout, though it cannot be called heavy. Of the limb-bones of *Astrapotherium*, I have seen complete examples only of the humerus, tibia, fibula, and, doubtfully, of the femur. In all three, slenderness and elongation are the characteristic features, which are in striking contrast to the size of the head and trunk.

No part of *Homalodontotherium* is more peculiar and bizarre than the hind feet, all the enigmas of which are by no means solved; perhaps, for want of the living animals, they are destined to remain insoluble. Except for the phalanges, and the vestigial first metatarsal, both hind feet of the Field Museum specimen are nearly perfect. The right pes lacks only the calcaneum, the left one has lost the cuboid, ento- and mesocuneiforms. By combining the two, it is easy to reconstruct the foot. In figuring the pes, Ameghino fell into a number of errors, which I adopted and perpetuated,[1] for want of means to correct them, adding some of my own. The discussion of the gait and manner of using the feet will be taken up in connection with the restoration (p. 26).

The *Tarsus* (Plate V, Fig. 19) is now completely known, so far as its anatomy is concerned; its physiology is another and much more difficult problem. The astragalus is fundamentally like that of the Toxodonta and the Litopterna, but

[1] Scott, '12, p. 280, Fig. 44.

with very marked peculiarities; aside from the neck, the bone is nearly square, with almost equal transverse and proximo-distal diameters. The trochlea is but indistinctly grooved and would be nearly flat, were it not that the elevation of the fibular border makes it slightly concave. The internal condyle has its articular surface extending proximally in a tongue-shaped facet, for which there is a corresponding surface on the distal end of the tibia, above described. The external border is also produced proximally, but not nearly so far, and these two proximal extensions are separated by a broad, triangular depression. The extensions are supported by a massive and rugose prolongation of the plantar surface, which thus projects proximally above or behind the trochlea. Into the depression between the articular extensions opens a small canal, which perforates the astragalus diagonally downward and forward, and opens on the plantar side into a deep fossa between the two facets for the calcaneum. This trochlea is highly characteristic; and those features, just described, are not found in any other order or suborder of Santa Cruz ungulates, in all of which the astragalus is known. On the external side of the trochlea is a very large surface for the fibula, which forms a rather obscure angle with the outer condyle; the surface for the internal malleolus of the tibia is much smaller, and curves gradually into the trochlea.

The neck of the *astragalus* is longer and more distinct than in the Toxodonta, and the head is much more distinctly set off by a constriction. This head is strongly convex, almost hemispherical. It articulates distally with the navicular, and has a lateral contact with the cuboid, a character which is very rare, if not unique, among the Santa Cruz ungulates. On the tibial side of the neck is a small articular surface, proximally continuous with the trochlea and distally with the navicular facet, which is, for a small surface on the distal end of the tibia, near the dorsal border, but is in contact with that surface only when the foot is extremely flexed upon the leg. On the plantar side of the astragalus are two large surfaces for articulation with the calcaneum. The external one is narrow and elongate, tongue-shaped, and contracting distally; it is simply concave in the proximo-distal dimension. The internal, or sustentacular facet is narrow and considerably more elongate than the external one, and is connected by a narrow articular surface with that for the navicular. Though rather complexly warped, this surface is convex, on the whole.

The *calcaneum* (Plate V, Fig. 19) is an extraordinary bone, very different in appearance, though not in the essentials of structure, from that of *Nesodon*. Proportionately very heavy and massive, it is, at the same time, very elongate, which is, of course, due to the great extension of the *tuber calcis*. Distally, the tuber is laterally compressed, but very deep in the dorso-plantar diameter. Proximally, the tuber broadens and the free end is very massive, club-like, and roughened. At the proximo-internal angle, on the plantar side, is a large rugosity, and at the distal end is another, but much smaller, rugosity on the plantar side of the cuboid facet. I think it very probable that these two prominences, at the proximal and distal ends of the calcaneum, supported the weight of the animal in walking. There is a second rugosity on the distal end, external to the cuboid surface, which, no doubt, served for ligamentous attachment.

The calcaneum, which is a very long bone, out of all proportion to the astragalus and other bones of the pes, has four large and very conspicuous articular surfaces; that for the fibula is exceptionally large, relatively more so than in any other Santa Cruz ungulate, and projects far out beyond the fibular side of the tuber. It is simply convex proximo-distally, very slightly concave transversely, and is so oblique that it presents internally and distally, when the fibula and calcaneum are in articulation. The joint is then seen to be a very peculiar one, which involves the partial rotation of the calcaneum on its long axis. The external surface for the astragalus is very large and presents obliquely inward and dorsally, forming a distinct angulation at the junction with the fibular surface. In *Nesodon,* the fibular facet is extended on the dorsal side of the tuber, a prolongation which does not occur in the present genus.

The sustentaculum is not very large proportionately, but massive and rugose on the plantar side; the surface for the astragalus is elongate, somewhat pear-shaped in outline, and narrowing distally to a bluntly rounded point. The facet for the cuboid is relatively small and concave in both dimensions.

The calcaneum and astragalus are, in appearance, very unlike those of *Nesodon;* the astragalus is much wider, with longer neck and more hemispherical head, and less distinctly grooved trochlea, while the calcaneum has a much longer tuber, which is more thickened and club-like at the free end. Apparently, there is no contact between the calcaneum and the navicular, such as exists in *Nesodon* and the Typotheria.

The *navicular* is a curiously shaped bone, quite unlike that of *Nesodon.* It is short proximo-distally, shallow planto-dorsally, and very wide transversely, extending internally to the astragalar surface, which is, itself, unusually wide. The tibial border is twice as long proximo-distally as the fibular, and is much thickened and roughened. The proximal surface for the astragalus is very wide transversely and deeply concave, and is so much wider than the head of the astragalus as to suggest considerable motion in this joint. The distal end of the navicular is but partially covered by the articular facets for the three cuneiforms, which, though forming a continuous surface, are yet clearly demarcated into three parts, bounded by angulations. The surface for the entocuneiform is very small and convex, that for the mesocuneiform is many times as large and of irregularly polygonal outline and obscurely warped surface. The facet for the entocuneiform is still larger and of oblong shape, with the principal dimension the dorso-plantar one. The fibular side of the navicular is occupied by the nearly plane and quadrate surface for the cuboid. The navicular has no contact with the calcaneum and no plantar hook.

The *cuboid* is a large, heavy, and peculiarly shaped bone, quite different from that of *Nesodon;* its principal diameter is the dorso-plantar, but the proximo-distal dimension is nearly as great; in width it increases distally, so that the lower end is the widest part. The articular surface for the calcaneum is large, convex, and very oblique to the long axis of the bone, and meets the navicular facet at nearly a right angle, which makes the dorsal face pointed proximally, an appearance altogether different from the squarely truncated proximal end of the cuboid

in *Nesodon*. Between the calcaneal and navicular facets is a narrow, articular band, which can only be for the astragalus. As already mentioned, the latter has considerable lateral play on the navicular and, when it moves as far as possible toward the fibular side, is brought into contact with the cuboid. This contact is entirely lateral, the astragalus not resting on the cuboid at all, as it does in nearly all Perissodactyla. The facet for the ectocuneiform is narrow proximo-distally, but it extends across the whole dorso-plantar diameter; between this and the surface for the navicular is a wide depression. The distal end is occupied by the facets for mts. IV and V, which are continuous. The plantar face of the cuboid is much roughened, and at the external angle is a short, blunt rugosity, which probably represents the usual hook.

In *Nesodon* the cuboid has an entirely different appearance; the dorsal face is quadrate, nearly square, with proximal and distal ends transverse and parallel. Viewed from the dorsal side, the cuboid seems to be smaller than the ectocuneiform, while in the genus before us it is much larger; the difference is, of course, referable to the tridactyl foot in one animal and the tetradactyl pes in the other.

The *entocuneiform* is not ankylosed with the mesocuneiform, as it is in *Nesodon;* in shape it is narrow and scale-like, and is much longer proximo-distally than the other cuneiforms. This bone carries three articular surfaces: a small, oblique, and slightly concave facet for the navicular is on the proximal end; below this, on the fibular side, is a much larger and decidedly concave facet for the mesocuneiform and, on the distal end, is a very small surface for mt. I, of which no example has yet been found, but the facet on the distal end of the internal cuneiform shows that the hallux cannot have been more than a nodular rudiment. Following Ameghino, I assumed[1] that the first metatarsal was functional, an inference from the presence of an articular surface on the tibial side of mt. II, for, at the time when I wrote, the ento- and mesocuneiforms were still unknown. The character of the former and, especially, the facet on the distal end, make it plain that this assumption was erroneous.

The *meso-*, or second, *cuneiform* is hardly half as long, proximo-distally, as the first, but is very much wider and heavier, with rugose and nearly square dorsal face. The ends and sides are almost covered by articular surfaces; proximally there is a relatively large, somewhat saddle-shaped facet for the navicular and, distally, a very similar and somewhat oblique surface for the head of mt. II. The tibial side is covered by a facet for the entocuneiform, and the fibular side by one for the ectocuneiform.

The *ectocuneiform* is a very large bone, nearly twice as large in linear dimensions as the median one, a very unusual disproportion in feet that have more than three functional digits; it, too, carries articular surfaces on all sides except the dorsal and plantar.

The *Metatarsus* (Plate V, Fig. 19) consists of four functional digits (mts. II-V) and, very probably, a nodular remnant of the first. This bone has not been recovered, but its former presence may be inferred from the facets on the ento-

[1] SCOTT, '12, *loc. cit.*

cuneiform and mt. II, though whether this rudiment was a nodule or a splint, cannot be positively stated. The functional metatarsals, II-V, are surprisingly short, less than half as long as the corresponding metacarpals and of an entirely different appearance. In length and diameter, they increase regularly from within outward, so that mt. II is the shortest and lightest, mt. V the longest and heaviest, of the series. There is very little interlocking of the metatarsals with one another, or with the tarsals. The head of mt. II rises a little higher proximally than that of mt. III and abuts against the tibial side of the ectocuneiform which has a facet for it; but the proximal articular surfaces of the other three members of the series (mt. III-V), when placed together in their natural positions, form a continuous and simply concave surface for articulation with the ectocuneiform and the cuboid. This is in marked contrast to the pes of *Nesodon*, in which the three metatarsals present, II, III, and IV, have their proximal ends at different levels and have lateral contacts with the tarsals, except that mt. IV, which is attached to the cuboid, has no such contact.

Metatarsal II, though disproportionately small in comparison with the metacarpals, is yet quite stout; the proximal end is narrow, but thick in the dorso-plantar dimension; it is occupied by the facet for the mesocuneiform, which is broad on the dorsal, narrowing to the plantar side. On the tibial side of the head is a small, but conspicuous, facet for the entocuneiform, and on the fibular side is a small surface for lateral contact with the ectocuneiform. Thus, mt. II is the only one of the series which has lateral contacts with the tarsals. The shaft is short and relatively stout; proximally, it is narrow and very thick, but becomes wider and thinner distally. The trochlea is low and asymmetrical; on the fibular side, the articular surface is a convexity, which becomes slightly concave on the tibial side. Above the trochlea, on the dorsal face, is a faintly marked concavity, with rugose proximal border, which is a slight suggestion of the remarkable articular concavity seen at the distal end of the shaft in the metacarpals, but the articular surface of the trochlea does not extend up into these metatarsal cavities. The carina is low and confined to the plantar side, not visible in front view, and is asymmetrically placed.

Metatarsal III is larger and stouter than II, though extremely short in comparison with mc. III. The proximal end is entirely covered by the ectocuneiform, which is unusually large. On the tibial side, near the dorsal border, is a small, irregularly ovate facet for the head of mt. II, while, on the fibular side, the facet for mt. IV occupies the whole dorso-plantar diameter. The shaft and trochlea are much as in mt. II, except for their larger size, and the trochlea is more nearly symmetrical.

Metatarsal IV is longer and stouter than III, and the facets for articulation with the metatarsals on each side are more prominently projecting. The shaft is longer and decidedly heavier and, below the head on the fibular side, is a conspicuous tuberosity. The trochlea is symmetrical, lower than that of mt. III, and the cavity above it is almost obsolete.

Metatarsal V is decidedly the longest and heaviest of the series, and much the most peculiar in appearance. The facet for the cuboid is very oblique, rising

higher on the fibular side, but, as mentioned above, it forms a continuous curve with the heads of III and IV. From the fibular side of the head is given off a very large and heavy process, with much thickened and rugose free end, greatly resembling the structure seen on the same metatarsal in all of the genera of Santa Cruz Gravigrada of which the foot is known, but not in the huge and massive genera of the Pleistocene. I know of no other hoofed animal which has such a metatarsal, which is much more edentate than ungulate in character. The shaft of mt. V is broader, but somewhat thinner, than that of mt. IV, and the distal thickening above the trochlea is much more prominent and rugose. The trochlea is low and asymmetrical, sloping down toward the fibular side. The carina is reduced to a minimum, and has almost disappeared.

Metatarsal II, length	M.0.066
Metatarsal III, length	.077
Metatarsal IV, length	.0854
Metatarsal IV, prox. width	.0273
Metatarsal V, length	.1026
Metatarsal V, prox. width	.0556

The *Phalanges* (Plate V, Fig. 20) of the pes are very scantily represented in the collection; only three are associated with this skeleton, one of the first and two of the second row, but no unguals. These phalanges are extremely small, very much smaller than those of the fore foot. The proximal phalanx and one of the second row would seem to belong to the fifth digit of the right side, and the other specimen of the second row to the same digit of the left pes. These bones are, therefore, presumably more asymmetrical than those of the other digits. The first phalanx has a decidedly oblique proximal end, corresponding to the distal trochlea of mt. V. The articular surface for the latter is simple, ungrooved, and not very deeply concave. The reflection of the articular surface over upon the dorsal side of the bone, which is so conspicuous on the first-row phalanges of the manus, is not present, and the two proximal rugosities on the plantar surface are relatively less prominent. In shape, this phalanx is very much as in the manus on a much smaller scale. The distal articular surface is very obscurely divided into two parts, and is transversely oblique in the same sense as the proximal one. Aside from size, the striking difference from the first-row phalanges of the manus is in their articular surfaces, proximal and distal.

The phalanges of the second row are extremely small; in bulk, as determined by weight, one of them is less than one-third of a corresponding one of the manus. The one assigned to the right side fits the proximal phalanx above described in a very perfect manner; it resembles a second row phalanx of the manus in form, but the articular ends are much simplified. The proximal surface is very obscurely divided into two concavities, of which that on the fibular side is the larger and deeper. A blunt, rugose projection arises from the externo-plantar angle, which I do not find in the manus, but this may be because no phalanges of digit V have been found in connection with that foot. The distal trochlea is simply convex, not showing any indication of the median groove which is so conspicuous in the fore foot, nor is the articular surface reflected nearly so far

upon the dorsal side as it is in the manus; evidently the claws could not have been flexed in anything like the same degree.

The unguals of the hind foot are still unknown; they must have been much smaller than in the fore foot, but there is no reason to suppose that, otherwise, they were different in any important way.

The material is still too incomplete to permit the making of a definitive reconstruction of this skeleton, and the figure (Plate VII) is no more than a preliminary attempt. Such attempts, however, serve a useful purpose in presenting succinctly what is known and what remains unknown of the skeleton in question. In the present instance, the uncertainty is chiefly that regarding the vertebral column; while the conformation of neck- and trunk-vertebrae is fairly well known, their number is still conjectural, and no example of the lumbar, sacral, or caudal vertebrae has yet been obtained. The drawing herewith presented would be greatly modified, could it be ascertained that the neck, trunk, and tail were much longer or much shorter than we have calculated. The skull, limb-girdles, limbs, and feet are quite completely known, so far as their skeletal elements are concerned, but much remains uncertain regarding the attitude, gait, and manner of using the curious feet. As already pointed out, there is no animal now in existence which has such a combination of characters, such seeming incompatibilities of teeth, skull, body, and feet, which might throw some light upon the habits and mode of life of these long-vanished creatures. It is especially noteworthy that no less than three different ungulate groups, the Entelonychia, Ancylopoda, and Agriochoeridae, should independently, I believe, have developed in this remarkable fashion. As shown in a subsequent section, these three groups were entirely unrelated, save as all the hoofed mammals may be derivatives of a common stock.

Aside from the length of the back-bone and of its various component regions, the principal uncertainty is as to the proper attitude of the feet in standing and walking. Filhol[1] restored the analogous *Macrotherium,* from the Miocene of France, as purely plantigrade in both fore and hind feet. The allied Ancylopodan genus *Moropus,* from the North American Miocene, is mounted by Holland and Peterson[2] as digitigrade, and Ameghino believed that in the Entelonychia, the feet rested by their external borders on the ground, bringing the palms and soles to face inwardly after the manner of the fore feet in the Ant Bear (*Myrmecophaga*) and all the feet of the Pleistocene Ground Sloths. In my former paper, in which I had only a few scattered foot-bones at my disposal[3] and had to depend upon the somewhat crude drawings in Ameghino's papers, I gave reasons for rejecting Ameghino's conclusion in favour of a digitigrade gait like that of *Moropus.* Now that I have the opportunity to examine well-preserved feet, both manus and pes, I am convinced that my former opinion should be much modified. As to the fore-foot, I am still convinced that Ameghino's suggestion is not acceptable; I can find no reason to think that this manus rested on the ulnar digit in walking; but, on the other hand, the question of plantigrade, or digitigrade, is by no means

[1] H. Filhol, '91, Pl. XLIII.
[2] W. J. Holland and O. A. Peterson, '14.
[3] Scott, '12, p. 271.

easy to answer. On the whole, the articulations seem to me to favour the digitigrade gait, the attitude which has been adopted in the restoration; but the manner in which the articular surfaces of the proximal carpals are carried over upon their dorsal faces distinctly suggests a plantigrade gait, much as in Filhol's figure of *Macrotherium.* Between these alternatives, I am unable to reach a definite decision.

Another difficult problem has to do with the use to which these strangely incongruous feet were put by the living animal. It is not necessary to suppose that in all three groups the feet were used in just the same way, but, so far as the Entelonychia are concerned, there is very strong reason to believe that these animals were fossorial in habit. Of course, this is not meant to imply that they were burrowers—their size would seem to preclude any possibility of that—but that they used the fore feet for digging, no doubt, in search of roots, tubers and other articles of food. Lydekker was, I believe, the first to suggest this, and he did so on the ground that the humerus resembled that of the Wombat in the great development of the deltoid crest and supinator ridge. As was previously stated, this humerus looks like that of a gigantic Mole.

Lydekker's inference is supported by several lines of evidence, of which he could have known nothing. Thus, the discoidal head of the radius is very different from that of any other known ungulate, and is certainly indicative of some degree of pronation and supination of the manus. Then, the joints between forearm bones and carpus, metacarpus, and phalanges are indicative of unusual freedom of motion. If the supposed presence of a clavicle should be confirmed, this would be additional evidence that the fore limb was used for purposes other than mere locomotion. Unintentionally, Lydekker weakened his own thesis by maintaining that Ameghino had erroneously attributed the ungual phalanges of the Gravigrade genus *Eucholoeops* to *Homalodontotherium.* He was misled to this conclusion by finding ungual phalanges of the ordinary hoofed-animal type attributed to the remains of the last named genus in the La Plata Museum collection. However, that was a mere accidental association, and it is now abundantly clear that Ameghino was right in his identification, and that the Entelonychia possessed claw-like hoofs of the Ancylopodan type.

So far as the hind foot is concerned, I am compelled to retract my criticism of Ameghino's views. As I had only drawings upon which to form an opinion, it seemed to me impossible to have the foot placed upon its fibular border without dislocation of the ankle joint. What I did not at all appreciate was the extraordinary mobility of the hemispherical head of the astragalus, which permitted a partial rotation of the hind foot upon the leg, and thus while still disagreeing with Ameghino as to the attitude and use of the manus, I have come to accept his views as to the pes, and in the restoration this is indicated. The figure makes plain the unusual disproportion between fore and hind feet which characterizes the present genus, and gives additional confirmation to Lydekker's hypothesis of fossorial habits. In nearly all burrowers, notably in the moles, the fore feet are powerful shovels, the hind feet relatively small and weak organs of locomotion. No other hypothesis so well explains the many extraordinary structural features of this animal as that of fossorial habits.

The skeleton is drawn in a crouching position, as though the animal were about to drink. Were the fore leg straightened, the figure would have considerable resemblance to that of *Moropus*, as restored by Holland and Peterson. The likeness to the Ancylopoda is undeniable, but I think it is a superficial one.

RELATIONSHIPS OF THE ENTELONYCHIA

Widely divergent views on this topic have been expressed by various paleontologists. Huxley,[1] in the very brief notice which forms the first mention of *Homalodontotherium*, speaks of it as "anoplotherioid," and Flower,[2] who had before him only the dentition, seems to regard it as related to the rhinoceroses. Such views are now obsolete, and need not be discussed; but the opinions of Lydekker, Ameghino, Roth and Schlosser should receive consideration.

Lydekker regarded all the indigenous South American groups of ungulates as more nearly related to one another than to any of the orders of the northern hemisphere, a conclusion which I cannot but accept. More specifically, he included Astrapotheria and Entelonychia in the same order, to which he gave the former group name. This classification has been followed by most subsequent writers, except Roth and myself. In Roth's[3] "epoch-making" paper, in which he proposed the superorder Notoungulata for all of the Santa Cruz hoofed-animals, except the Litopterna and the Astrapotheria, he founded his classification upon the remarkable structure of the auditory region. The Entelonychia, which agree with the Toxodonta in this regard, are thus widely separated from the Astrapotheria. Schlosser,[4] who accepted Roth's classification in the main, believes that the Astrapotheria should, nevertheless, be included in the Notoungulata.

Ameghino was the first to include *Homalodontotherium* and its allies in a special order, to which he gave the name Entelonychia. Subsequently, however, he abandoned this term and referred these genera to the Ancylopoda, a step which, so far as I am aware, has not been followed by any other writer. Thanks to Mr. Riggs' discovery, it is now possible to make a detailed comparison of all the significant parts of the skeleton in *Moropus* and *Homalodontotherium*. Such a comparison shows that, beyond a certain general likeness and the possession of clawed feet, the two groups are widely and fundamentally separated. The Ancylopoda are unmistakable perissodactyls which can, at most, be given subordinal rank. Their teeth are most like those of the Titanotheriidae, and all parts of the skeleton, especially the all-important tarsus, are typically perissodactyl, save only the metapodials and phalanges, which are peculiarly modified.

The Entelonychia, on the other hand, have no perissodactyl characters, and the points in which they most resemble the Ancylopoda are just those in which the latter depart most widely from the perissodactyl type. In other words, both groups have undergone a similar modification of the feet, but from different starting-points. As Roth pointed out, the very remarkable character of the

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[1] T. H. Huxley, '70, p. lvii.
[2] W. H. Flower, '84, p. 173.
[3] S. Roth, '03.
[4] M. Schlosser, '18, p. 325.

auditory apparatus in the Entelonychia is unquestionably toxodont, and the same is true of the dentition. When unworn molars are examined, it becomes evident that they conform fundamentally to the toxodont plan, though, of course, with modifications. The incisors and canines are different, for the incisor tusks of *Nesodon, Toxodon,* etc., are wanting, and the canines, though small, are yet more tusk-like than the incisors. The skeleton of the Entelonychia, it is true, departs widely from that of the Toxodonta, but there is a fundamental similarity, and the departures from a common plan are such as were made necessary by the adaptation to fossorial habits.

It is now possible, as never before, to institute a comparison between the feet of the Entelonychia and those of the Astrapotheria, for in the collections of Field Museum are excellent examples of the fore and hind feet of *Astrapotherium,* which show that the manus which I figured[1] and, with extreme doubt, referred to one of the Astrapotheria, was correctly so referred, as were also the calcaneum[2] in the Ameghino collection and the astragalus figured by Schlosser.[3] The manus which is shown in my paper is a composite made up from a photograph of a fore foot from the Deseado formation, which Ameghino assigned to *Pyrotherium,* and from Tournouër's[4] drawing, which he believed to be referable to *Astrapotherium,* also of the Deseado formation. The matter was so very doubtful, that I had but little confidence in Tournouër's identification and said almost nothing of this individual in the text, especially as Professor Loomis[5] was inclined to accept Ameghino's identification as against that of Gaudry and Tournouër.[4] It now appears, however, that the latter were right, for there can be no possible doubt concerning the Field Museum individual, which was found in Santa Cruz beds (where remains of *Pyrotherium* have never been obtained) in association with a skull and parts of the skeleton, all clearly belonging to a single individual.

A comparison of the feet of *Astrapotherium* with those of *Homalodontotherium* immediately shows that the two genera have hardly anything in common and that in the whole series of Santa Cruz ungulates there are no two groups in which the feet are more unlike. In *Astrapotherium,* as is well shown in the figures of Tournouër and myself, the manus is surprisingly Proboscidean in appearance, the pes somewhat less so, but both fore and hind feet have certain remarkable peculiarities not found in any other known group of ungulates. In my figure there is one important error for which I cannot account: the first metacarpal has been lost and a phalanx substituted for it.

It is not my purpose to give a detailed description of these most interesting and important specimens, but merely to indicate, in a general way, their salient characteristics, as compared with those of the Entelonychia.

The fore foot suggests that of a small elephant, though with characteristic differences. The carpus is very low proximo-distally, but very wide transversely, and the arrangement of its elements is almost taxeopod. The scaphoid rests

[1] Scott, '28, Pl. XXXVI, Fig. 6.
[2] *Ibid.*, Pl. XXXVII, Figs. 3, 3a.
[3] *Op. cit.*
[4] A. Tournouër, '05, p. 306.
[5] F. B. Loomis, '14, pp. 172-73.

upon both trapezium and trapezoid, but is widely removed from the magnum, while the lunar overlaps upon the unciform. Tournouër's figure is very remarkable in one respect, in that it shows the trapezium as being far removed from the scaphoid and touching only the trapezoid, from which it stands out almost at a right angle. This gives the first digit the appearance of being an opposable thumb. There is nothing like this to be seen in Ameghino's specimen or in that of the Field Museum collection, and it remains to be seen whether this arrangement of the bones is erroneous or not. There are five fully formed and functional digits and the metacarpals, of which the fourth and fifth are imperfect distally, would seem to have all been approximately of the same length. In transverse width, they increase regularly and markedly from the second to the fifth, but, in the Deseado genus they are of more uniform width.

This is a point of resemblance to *Homalodontotherium*, but it has little significance in view of the very great dissimilarity of these bones in the two genera. In *Astrapotherium*, the metacarpals are short, hardly half as long as those of *Homalodontotherium*, very broad transversely, especially mc. III-V, and thin palmo-dorsally. There is a little more carpo-metacarpal interlocking than in the last-named genus, for the magnum, which in *Homalodontotherium* has but a small lateral contact with mc. II, rests directly upon the head of that bone. A very peculiar feature is that the head of mc. V extends up to a contact with the cuneiform, which has a large facet for it. The distal ends of the metacarpals are of the type common among the polydactyl ungulates and totally different from the extremely peculiar mode of articulation seen in *Homalodontotherium* and described in the foregoing pages. The trochlea is very low and simply convex. Unfortunately no ungual phalanges have been recovered, but there can be little doubt that these were hoofs, not claws.

The hind foot of *Astrapotherium* is much less elephantine in character than is the fore foot, the specifically Proboscidean features being absent. Thus, the astragalus, which has been well figured by Schlosser, extends over the whole dorsal surface of the calcaneum, excluding the latter from any contact with the fibula, and the calcaneo-cuboidal articulation is very limited and of very exceptional type. The astragalus covers nearly the whole proximal side of the cuboid, upon which the navicular does not extend at all. Perhaps the most exceptional and characteristic feature of the Proboscidean tarsus is the extension of the navicular over the cuboid, thus widely separating the latter from the astragalus. No indication of this is seen in *Astrapotherium*. While there is no such disproportion in size between fore and hind foot as there is in *Homalodontotherium*, there is yet a difference; the pes is about as much smaller as it is in the elephants.

The *astragalus* has some resemblance to that of the Amblypoda of the North American Eocene, but the likeness is superficial; the bone is short and broad, with nearly flat trochlea, made slightly concave by the elevation of the fibular border and the articular surface is, on the tibial side, extended proximally in a tongue-shaped process, somewhat as in *Homalodontotherium*, almost the only likeness in the pes of the two genera. There is no canal perforating the astragalus. This bone has practically no neck and the head is utterly unlike

the hemispherical one of *Homalodontotherium;* it is very broad, convex transversely, but having only a very slight dorso-plantar curvature. This head rests upon the navicular and the large cuboid surface is more upon the neck than upon the head.

The *calcaneum* is somewhat distorted by crushing, and the description which I have elsewhere given of the isolated calcaneum in the Ameghino collection may well be reproduced here: "The calcaneum is very peculiar and quite unlike that of any ungulate with which I have been able to compare it. . . . The external facet for the astragalus is very large, elongate proximo-distally, rather narrow transversely and decidedly convex in both directions; between this facet and the sustentaculum is a deep fossa. The sustentaculum is large, prominent and extremely massive; seen from the dorsal side, it has a nearly quadrate outline and the astragalar surface, though continuous and covering the entire dorsal aspect of the process, is yet quite distinctly divided into proximal and distal concavities. The facet for the cuboid is of very exceptional character; it is divisible into two portions, of which the outer may be considered the principal one, but is remarkably small; it covers but little of the distal end of the calcaneum and presents internally as much as distally. Continuous with this is a narrow articular band along the distal margin of the sustentaculum. . . . The portion of the calcaneum which is distal to the sustentaculum is very short and, on the plantar side, extremely massive; from the fibular side is [given off] a very prominent and heavy projection, doubtless for ligamentous attachment. The tuber is short and very heavy. No other known Santa Cruz mammal has a calcaneum even remotely resembling this; the lack of any facet for the fibula, the shape and position of the cuboid facet, the form of the sustentaculum and the distal external projection are all unique features."[1]

At all events, the calcaneum of *Homalodontotherium* is completely unlike that of *Astrapotherium.* It is not necessary to repeat the description already given (see p. 21); it will suffice to mention the principal points of contrast. In *Homalodontotherium* the tuber is very elongate and its free end is greatly widened, thickened and club-like; there is a very large and conspicuous fibular facet, so broad that it projects shelf-like from the external side of the bone. The cuboid contact is of the normal type, the calcaneum covering the whole proximal end of the cuboid, which touches the astragalus only laterally.

The *navicular* of *Astrapotherium* is very broad, projecting much internally beyond the ectocuneiform, and extremely short proximo-distally, being hardly more than a curved plate, of which the surface for the astragalus is deeply concave. On the distal side are three obscurely demarcated facets for the cuneiforms, that for the internal one being much the largest. The cuboid, when in its natural position and seen from the front, appears to be much smaller than the ectocuneiform; when taken out, it is seen to be much larger, for its principal diameter is the dorso-plantar; its proximal end is covered by the astragalus and the calcaneal facet is on the fibular side. If, as was probably the case, there was a facet for the sustentaculum, it has been eaten away. . . .

[1] Scott, '28, pp. 330-31, Pl. XXXVII, Figs. 3, 3a.

Of the three cuneiforms, the internal one is much the largest and the median one is much reduced, except in the dorso-plantar diameter. In *Homalodontotherium* the ectocuneiform is the largest and heaviest of the series.

The *metatarsus* of *Astrapotherium* is one of the most bizarre features of a very bizarre animal; it consists of five complete members, the relative sizes of which are unlike those of any mammal that I have seen. Only of mt. IV and V are the distal ends preserved; mt. III is so far complete that its length may be closely estimated, but the others (I and II) have lost a fourth of their length. The first metatarsal is the broadest of the five, but has no great dorso-plantar diameter; it articulates only with the entocuneiform. Metatarsals II and III are so slender and shrivelled-looking that they would suggest a pathological state, were it not that the foot of the other side shows them to be normal. Metatarsal IV is almost certainly the longest of the series and the stoutest; not quite so broad as mt. I, its proximal end has a remarkable dorso-plantar extension; it is covered entirely by the cuboid, not as in *Homalodontotherium*, articulating with the ectocuneiform.

Metatarsal V is extremely peculiar and looks more like the calcaneum of a Santa Cruz ground-sloth thana normal metatarsal: with a head no wider than that of mt. IV, the shaft expands into a broad plate, with convex dorsal and deeply sulcate plantar face. The Gravigrade-like projection from the fibular side, near the proximal end, which is so conspicuous in *Homalodontotherium*, is not present. The distal trochlea has been lost. In *Homalodontotherium* the proximal ends of the four functional metatarsals form a regularly curved, transversely concave surface, only the head of mt. II rising slightly above the others, but there is no such regularity in the pes of *Astrapotherium;* the heads of mts. IV and V extend proximally considerably higher than those of II and III, while that of I is much lower than the latter.

The first and second phalanges of the much-reduced digit II have been recovered; they are surprisingly small, slender, depressed and somewhat equine in appearance. They are totally different in every respect from those of *Homalodontotherium.*

We are now in a position to come to some definite conclusion concerning the genetic relationships of the Entelonychia. The materials essential to such a conclusion are before us, as all of the Santa Cruz ungulate groups are so far known, that future discoveries are not likely to add much of essential importance. I am inclined to agree with Lydekker in believing that all the Santa Cruz ungulates are interrelated and derived from a common stock, but I cannot follow him in referring the Astrapotheria and the Entelonychia to the same order, still less suborder. Lydekker was misled by the inclusion among the La Plata Museum Entelonychia of ungual phalanges of ordinary hoofed-animal type, and he knew nothing of the foot-structure in either group. It is now abundantly clear that the inclusion of these unguals (presumably of *Nesodon*) was due to an accidental association. Roth was the first to point out that *Homalodontotherium* was essentially toxodont in affinities and he, therefore, included it in his Notoungulata, from which he excluded the Astrapotheria and the Litopterna. This new material

fully confirms Roth's view and demonstrates the wide and complete separation of the Entelonychia from the Astrapotheria.

It would serve no useful purpose to make a detailed comparison between the Ancylopoda and the Entelonychia. The monograph of Holland and Peterson on *Moropus* conclusively shows that these animals are only aberrant Perissodactyls and that they cannot be related to their South American analogues. The Entelonychia evidently stand in the same relation to the Toxodonta as the Ancylopoda do to the Perissodactyla. They arose from primitive pentadactyl toxodonts, retaining a common plan of molar and cranial structure, but undergoing remarkable modifications of limbs and feet in adaptation to a fossorial habit of life.

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NEW CARNIVOROUS MARSUPIALS

FROM THE

DESEADO FORMATION OF PATAGONIA

BY

William J. Sinclair

Through the kindness of the late Director D. C. Davies and Mr. E. S. Riggs, Associate Curator of Paleontology of Field Museum of Natural History, I have had the privilege of determining the South American fossil marsupials secured by the Marshall Field Paleontological Expeditions to Argentina and Bolivia under Mr. Riggs' leadership. Several of the better known Santa Cruz species are represented by well-preserved skulls and jaws, but these do not add materially to what has already been published in Vol. IV, Part III, Reports of the Princeton University Expeditions to Patagonia, Mammalia of the Santa Cruz Beds, Marsupialia, except to demonstrate that the lower jaw halves may be entirely separate in young adult individuals of *Borhyaena.*

A skull of this genus from the Deseado horizon (Astraponotus beds) at the southern end of Lake Colhue Huapi is, however, unique and, so far as can be ascertained from the literature available, is probably an undescribed form which may be designated *Borhyaena riggsi* in recognition of Mr. Riggs' kindness in extending to me the initial invitation from Field Museum to examine the marsupial material secured by his parties. The type specimen is No. P 13433, Field Museum of Natural History. It is a skull lacking basicranium, parts of both arches, the premaxillae and most of the palate. It was evidently in pieces when found and, in its present condition, has undergone considerable reconstruction. With the exception of the incisors and the last right molar, the dentition is complete and little worn.

As shown in Plate VIII, Figs. 1 and 2, the upper canine has a large, swollen base with a shallow groove on the inner side and a thick, pointed crown, unworn anteriorly by contact with the lower canine, but with the corresponding posterior margin worn from the tip to the base of the enamel. Just how this was accomplished is not clear. The more pointed canine, in contrast with the thick, blunt crown figured[1] in Santa Cruz representatives of the genus, is undoubtedly due to its less worn condition. All the premolars are double-rooted and increase in size posteriorly. They are so closely crowded that the anterior premolar is in contact with the canine and has its crown placed transversely with respect to the long dimension of the tooth row. It is both smaller and more transversely placed than in the Santa Cruz borhyaenas, both perhaps valid specific characters. The crown has a blunt central cusp and a very low heel, which,

[1] Princeton Patagonian Reports, Vol. IV, Pt. III, Pls. XLIV, XLV.

owing to the transverse position of the tooth, is internal instead of posterior. The median premolar is larger, with blunt central cusp and prominent heel continued as a cingulum about the rear of the crown, both externally and internally, where the tooth widens out considerably. It is almost a duplicate of the posterior premolar which has a much larger and higher crown with a broader heel-ledge extending around the rear of the tooth on both outer and inner sides. The high, blunt tip of the principal cusp is quite unworn. The molars are either entirely unworn or but little worn, corresponding teeth varying in this respect on opposite sides of the palate. They increase in size posteriorly from the first to the third, all of which have the protocone faintly indicated, but retain a stout inner root. The paracone is small, greatly exceeded by the metacone which is high and pointed, with outwardly directed metacone spur. The anteroexternal style is prominent, limiting anteriorly a broad, shallow concavity on the outer surface of the tooth, particularly noticeable in $m^{\underline{3}}$. The last molar ($m^{\underline{4}}$) is double-rooted with but two cusps on the crown, the paracone and anteroexternal style, separated by a shallow notch and forming a transverse shear.

The tooth row is much straighter than in any of the Santa Cruz borhyaenas, but I am in doubt as to how much of this is due to crushing, as the skull has, obviously, been deformed laterally, resulting in arching up the profile above the orbits and along the median junction of the nasals (Plate VIII, Fig. 1), and affecting the lateral expanse of the arches. The premaxillae have been restored to agree in a general way with their configuration in the Santa Cruz species, but a fragment of the ascending process on the left side indicates that the notch for the accommodation of the tip of the lower canine was by no means as deep as in them, nor was the muzzle as greatly expanded in the region of the canine alveoli. The proportionately greater length of the face in front of the orbits, in comparison with the Santa Cruz species, as shown in Plate VIII, Fig. 1, is undoubtedly due to deformation and considerable reconstruction is involved on the side shown in the drawing. It is much shorter on the other side. The nasals are greatly expanded posteriorly as in the Santa Cruz species, but the parts preserved do not make contact with either the frontals or the lachrymal, considerable plaster reconstruction intervening. The interorbital tract is slightly more convex than in the Santa Cruz borhyaenas, due to deformation. Postorbital frontal processes are lacking in all, and in *B. riggsi* the temporal ridges are very faint, soon fading out anteriorly. The sagittal crest is entire and shows the same depression in the parietal region as in the well known Santa Cruz species. Enough of the lambdoidal crest remains to assure the correctness of its semicircular outline, as in the Santa Cruz borhyaenas and, as in them, the parietal extends to the margin of the crest, excluding the supraoccipital from the upper surface of the skull. The orbits are smaller than in the Santa Cruz species and are placed as far forward as in them, lying approximately above the middle of the second molar. The infraorbital foramen is farther forward on the left side (Plate VIII, Fig. 1) than on the right where it opens on a line with the junction of the posterior premolar and first molar. There is a large

lachrymal tubercle on the orbital rim, back of which the lachrymal duct opens within the orbit. The zygomatic arches are very heavy and had, originally, much greater lateral expanse than is indicated in the drawing (Plate VIII, Fig. 1) where they are shown in their present deformed condition. Postorbital jugal processes are but slightly indicated, but the jugal bar extends backward to the glenoid fossa which it bounds anteriorly. The base of the skull is lacking and so much reconstruction enters into the palate that little can be determined regarding it except to note the presence of two deep pits between molars $^{\underline{2}}$ and $^{\underline{3}}$, and $^{\underline{3}}$ and $^{\underline{4}}$, respectively, for the reception of the elevated protoconids of the last two lower molars. In the Santa Cruz borhyaenas only the last depression is at all striking, the anterior one being but barely indicated. As in these forms, large postglenoid foramina are present.

The new form throws no light on the much debated origin of the South American marsupials. Since the Santa Cruz representatives of the Thylacynidae as I have termed them (or Borhyaenidae as Loomis[1] prefers to call them) were described in Vol. IV, Part III, Princeton Patagonian Reports, Mr. Heber A. Longman,[2] Director of the Queensland Museum, Australia, has issued an important paper on the zoogeography of marsupials[1] in which he suggests convergence in explanation of the striking resemblances between the Patagonian "sparassodonts" and the existing Tasmanian *Thylacynus*. Mr. H. E. Wood,[3] who also has reviewed the subject, is unable to find any direct evidence of "parallelism" and reaffirms the closest structural relationship of the "sparassodonts" with *Thylacynus*. Both papers contain extensive bibliographies. A typical *Borhyaena* from the Deseado might be expected to show more primitive features than any of the Santa Cruz representatives of the genus, but on the contrary, it seems to be still more specialized in the smaller size and almost completely transverse position of the anterior premolar. Although no lower jaw is present, there is every reason to believe that its dentition would have been typically borhyaenid and so easily separable from the various Deseado genera known mostly from the lower jaw.[4]

Measurements

Skull, length as restored, premaxillae to lambdoidal crest MM.	208
" width across jugal arches, approximate...........	132+
" least width of brain case........................	28.5
Upper dentition, length, canine to m$^{\underline{4}}$ inclusive, right side	80
" " " " " " " left "	84
Canine, anteroposterior diameter at base...............	15.5
" transverse " " "	11
Anterior premolar, anteroposterior diameter of crown (in this tooth measured in a direction transverse to elongation of tooth row)............................	7.5

[1] F. B. Loomis, The Deseado Formation of Patagonia, pp. 210-219, 1914 (illustrated).

[2] H. A. Longman, Memoirs of the Queensland Museum, Vol. VIII, Part I, 1924.

[3] H. E. Wood, Bulletin of the American Museum of Natural History, Vol. LI, pp. 77-101, 1924.

[4] Florentino Ameghino, Mammifères crétacés de l'Argentine, Deuxieme Contribution a la Connaissance de la Faune mammalogique des Couches á Pyrotherium, Boletin del Instituto Geografico Argentino, Tomo XVIII, 97-100, 1897 (illustrated).

Anterior premolar, transverse diameter (in this tooth measured in a direction coincident with that of tooth row)	MM. 3.5
Median premolar, anteroposterior diameter	9
" " transverse " maximum	6
Posterior premolar, anteroposterior diameter	10.5
" " transverse " maximum	8
M^{1} anteroposterior diameter	11
" transverse "	8
M^{2} anteroposterior "	13
" transverse "	9
M^{3} anteroposterior "	13
" transverse "	11.5
M^{4} anteroposterior "	5
" transverse "	10

In addition to the *Borhyaena* just described, two other specimens of marsupial carnivores from the Deseado formation have been sent to me for examination and description, by Field Museum of Natural History, through the kindness of Mr. E. S. Riggs, by whose expeditions they were secured. Both are from the Astraponotus beds of Ameghino, at the southern end of Lake Colhue Huapi, and consist of incomplete lower jaws. In the absence of more diagnostic material, it does not seem desirable to assign specific names to them, although the generic reference appears to be clear and both are undescribed.

The anterior half of a left mandibular ramus, No. P 13526, Figs. 3, 3a, Plate VIII, is referred to *Proborhyaena*, but to a smaller form than P. *gigantea* Ameghino, and affords a few additional characters for the separation of this genus from the vastly better known *Borhyaena*. Although the jaw is somewhat larger than in *Borhyaena tuberata* of the Santa Cruz, the premolars are more closely crowded, the anterior tooth occupying a position completely transverse to the long axis of the jaw, the second tooth placed obliquely and only the rear premolar having the anteroposterior alignment as in *Borhyaena*, from which it differs in proportionately smaller size and more strongly developed posterior cusp, but agrees in the swollen crown and elevated main cusp. A further difference appears in the equality of its crown length with that of the median premolar, although exceeding the latter in breadth, whereas in *Borhyaena* the median premolar is both shorter and narrower than the posterior one. In the specimen under discussion, the crowns of the anterior and median premolars have been damaged by fracture after fossilization, whereas that of the first molar was broken by use during life and only the worn stub of the posterior root remains. The second and third molars are also much worn. They probably resembled the corresponding teeth in *Borhyaena*,[1] but the heel cusp on the second molar is less strongly developed than in *Borhyaena*. In m_{3}, the crown pattern is almost entirely obliterated by wear. The canine is a much worn stub, but has the swollen base and inwardly grooved crown as in *Borhyaena*. Three incisors were present, the median

[1] Reports of the Princeton Expeditions to Patagonia, 1896-1899, Vol. IV, Part III, Pl. XL, XLV, Fig. 3.

displaced posteriorly with reference to the other two. The jaw symphysis is fused at the alveolar margin but quite free elsewhere. Much less dependence as a generic character can be placed on the fused or ligamentous union of the symphysis than is indicated in Loomis' generic key,[1] for the Field Museum collection contains a young mandible of a typical *Borhyaena* from Santa Cruz beds in which the symphysis is quite unfused. On the outer side of the jaw five mental foramina appear and there may have been others. These vary in number and position in *Borhyaena* and probably did so here also.

As generic characters, the greater depth of the jaw, correlated with the crowding of, and different proportions among, the premolars, will serve to further separate *Proborhyaena* from *Borhyaena* which it probably resembled in skeleton and habits.

The depth of the horizontal ramus below the middle of the third molar is 41 mm., decreasing to 34.5 mm. below the middle of the worn-out first molar. The crowded premolar series occupies a length of 28 mm. and the distance from the anterior premolar, which is in close contact with the canine, to $m_{\overline{3}}$ inclusive is 61 mm. The canine stub measures 19.5 mm. by 12.5 mm. at its base and the posterior premolar, at the base of the enamel, is 10.5 mm. anteroposteriorly by 6.5 mm. transversely at its widest posterior part measured at the enamel edge. Including the roots, the posterior premolar is 11.5 mm. anteroposteriorly, as is also the median tooth.

The genus *Cladosictis* has not hitherto been recorded from the Deseado but seems to be indicated unquestionably by both horizontal rami of the lower jaw, No. P 13521, Plate VIII, Figs. 4, 4a. It is larger than either of the two species of *Cladosictis* (*C. lustratus, C. petersoni*) illustrated in Vol. IV, Part III, of the Princeton Patagonian Reports referred to above, but agrees with *Cladosictis* in the characteristic spacing of the premolars, in their increase in size posteriorly, in the absence of metaconids in the lower molars and in the shape of the molar heels which, in their worn condition as preserved, consist of rounded eminences without basins. The rami are united at the symphysis by ligamentous suture and there are two large mental foramina, one beneath the anterior premolar and another below the junction point of $m_{\overline{2},\overline{3}}$, but an additional foramen is present below the anterior root of $m_{\overline{1}}$ on the right side and their number and position are probably not of much diagnostic importance. Both canines are broken off and the symphysial border and all teeth anterior to them are missing.

The dental series from the anterior premolar to $m_{\overline{4}}$ inclusive has a length of 72 mm.; the four molars alone occupy a space of 37.5 mm.; while the horizontal ramus has a depth of 17 mm. below the anterior premolar, 18.5 mm. below the posterior root of the posterior premolar and 22 mm. below the middle of the last molar.

[1] Loomis, The Deseado Formation of Patagonia, p. 212.

EXPLANATION OF PLATE I

Homalodontotherium segoviae Ameghino.

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Fig. 4, First Thoracic Vertebra, front view.	9
Fig. 5, Thirteenth(?) Thoracic Vertebra, front view.	9

Figures from specimen No. P 13092, Field Museum of Natural History, × 3/5.

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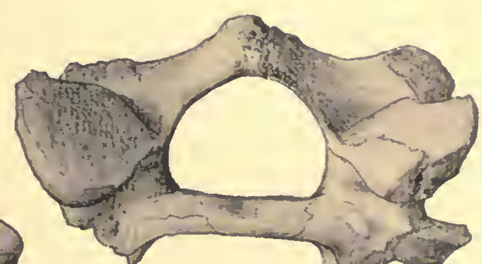

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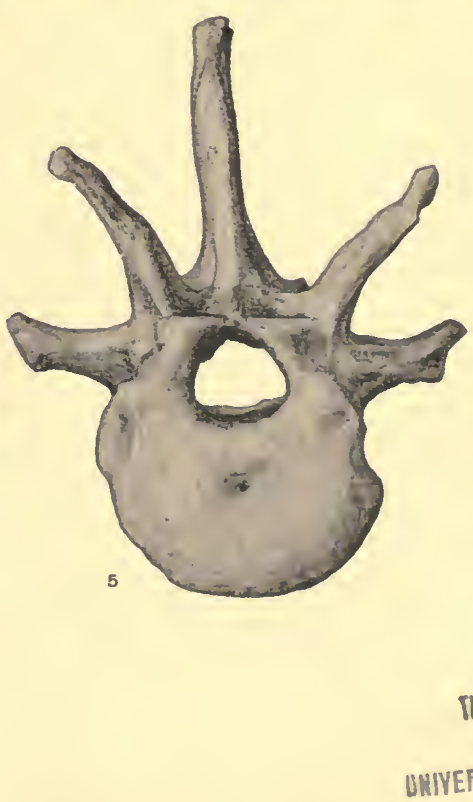

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PLATE II

EXPLANATION OF PLATE II

Homalodontotherium segoviae.

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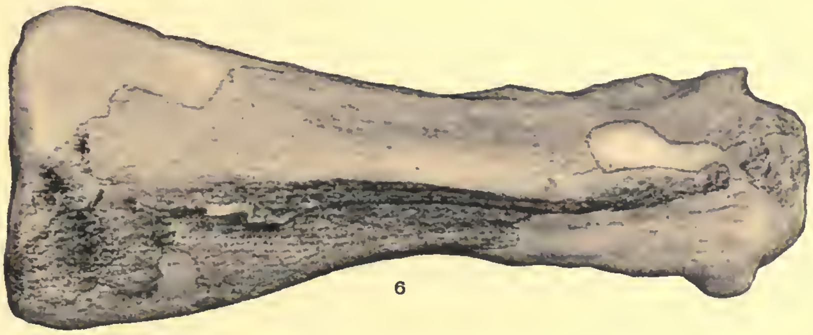
Fig. 9, Clavicle(?) anterior view.	10
Fig. 9a, The same, posterior view.	10

Specimen P 13092, Field Museum of Natural History.

All of the above figures $\times$ 1/2.



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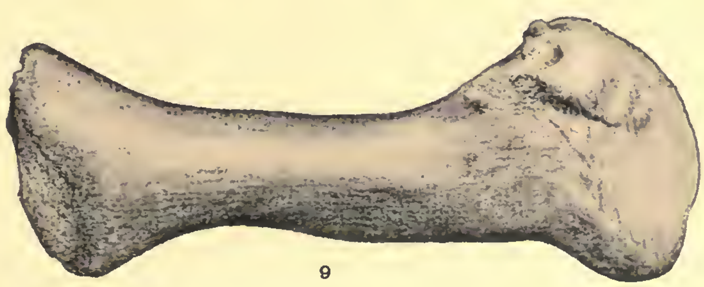

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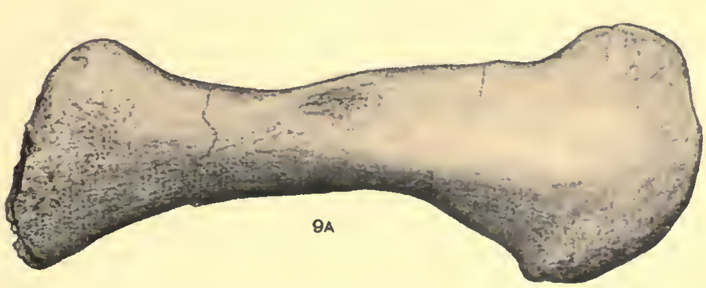

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PLATE III

EXPLANATION OF PLATE III

Homalodontotherium segoviae.

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Fig. 14, *Moropus elatus*, Phalanges of third digit, from the side.	18

All of the above figures $\times$ 3/5.

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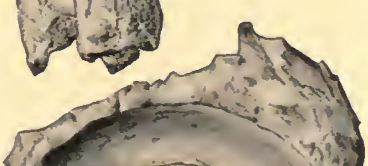

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PLATE IV

EXPLANATION OF PLATE IV

Homalodontotherium segoviae.

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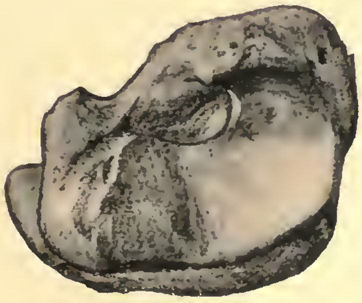

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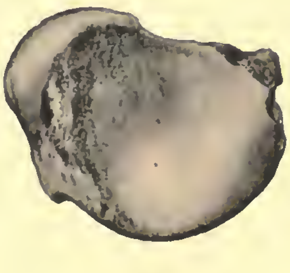

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PLATE V

EXPLANATION OF PLATE V

Homalodontotherium segoviae.

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PLATE VI

EXPLANATION OF PLATE VI

Homalodontotherium segoviae.

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Specimen P 13092, Field Museum.

All of the above figures, × 3/5.

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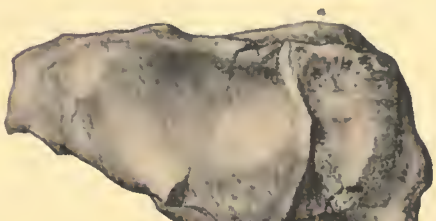

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PLATE VII

EXPLANATION OF PLATE VII

Homalodontotherium segoviae.

	PAGE
Restoration of the skeleton, seen from the left side; the animal is shown as though preparing to drink.	26

This figure is based chiefly upon the Field Museum specimen, No. P 13092, × 1/5.

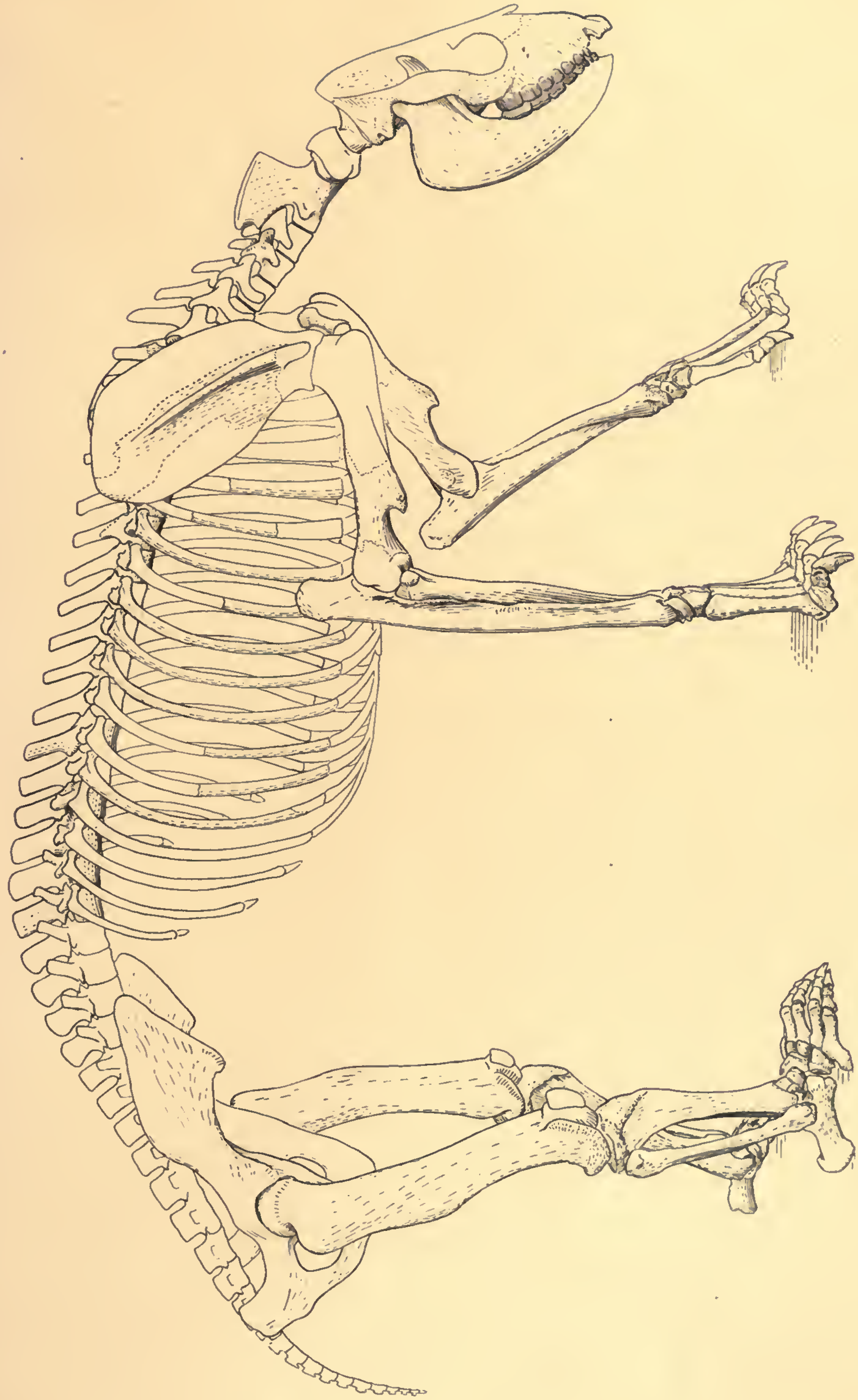

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PLATE VIII

EXPLANATION OF PLATE VIII

Borhyaena riggsi, sp. nov.

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The above figures are from specimen No. P 13433, Field Museum of Natural History.

Proborhyaena sp.

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Fig. 3a, Top view, ramus of mandible, × 1/2.	38

The above figures are from specimen No. P 13526, Field Museum of Natural History.

Cladosictis sp.

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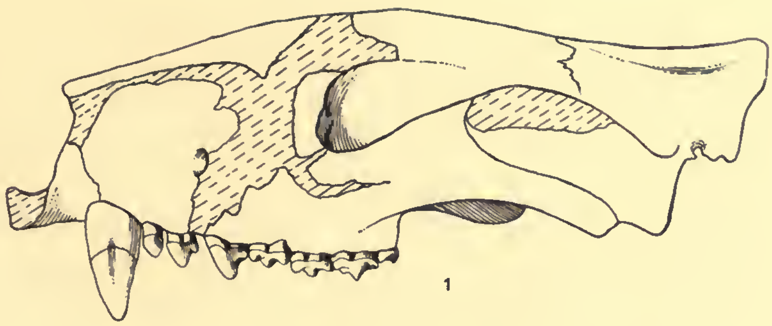
The above figures are from specimen No. P 13521, Field Museum of Natural History.



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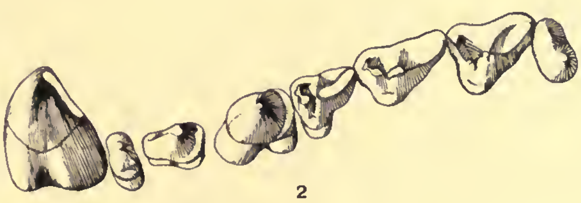

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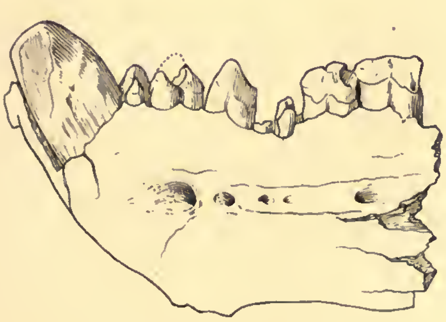

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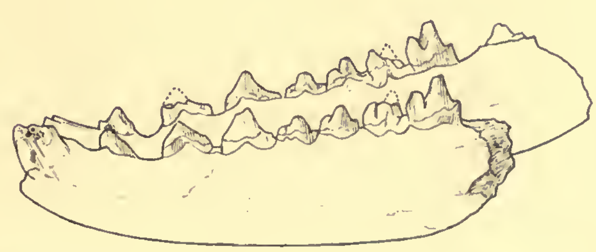

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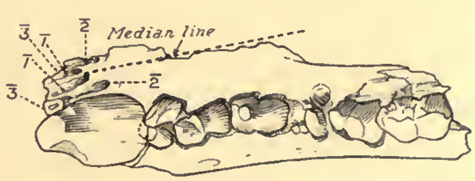

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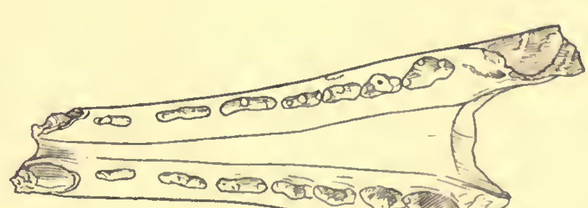

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